

## COMPETITION AND COEXISTENCE OF ANTS IN A SMALL PATCH OF RAINFOREST CANOPY IN PERUVIAN AMAZONIA

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*Abstract.*—A structurally complex patch of forest canopy in Manu National Park (Peruvian Amazonia), consisting of two trees and eleven associated vines, was sampled using insecticidal fog. Approximately 62,000 ants were collected and sorted to species. The total biomass (dry weight) of adult ants in the sample was close to 49 g. *Dolichoderus bispinosus*, the dominant species in the sample, made up 64.2% of the ant biomass and 69.0% of the individual ants. The four most abundant species (*Dolichoderus bispinosus*, *Dolichoderus decollatus*, *Azteca* sp. 1, and *Paraponera clavata*) together comprised nearly 95% of the biomass and individuals in the sample. In spite of the clear dominance of the sample by a few species, a total of 85 species in 29 genera were found, making this the most species-rich point sample of a canopy ant fauna ever documented.

Sampled at the level of a small number of trees, the rainforest canopy ant fauna reveals a pattern of remarkable species richness accompanied by strikingly low equitability in the rank-abundance distribution, or ecological diversity. A small number of species overwhelmingly dominate the ant assemblage but fail to exclude other ant species. Competition appears to limit the number of dominant species that can coexist in small areas, but a large majority of species present do not compete with the dominants and exist to a greater or lesser extent independently of them. The low ecological diversity observed in the sample may be in part a function of the spatial scale of sampling, and increased sampling should lead to a change in this pattern. The extent to which the species abundance distribution would become more equitable cannot be determined at this time. Finally, the structural complexity of the canopy may promote high species richness by creating microhabitat-linked species associations that effectively function as separate, non-competing ant assemblages.

*Key words:* Formicidae, ants, rainforests, ecology, Amazon, Peru, canopy, biological diversity.

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Until recently, information on the biology of arboreal ant assemblages was derived from isolated observations and sporadic collections carried out on treefalls. With the development of canopy fogging (Erwin, 1989a), more precise information has been gathered about the relative importance of ants in canopy arthropod communities (Moran and Southwood, 1982; Erwin, 1983b; Adis *et al.*, 1984; Majer *et al.*, 1990; Stork, 1991; reviewed by Tobin, 1995) and about the taxonomic composition of canopy ant assemblages (Wilson, 1987; Harada and Adis, 1994; Tobin, ms.; Tobin and Cover, ms.). The next logical stage in the examination of canopy ant assemblages involves characterizing them in terms of the relative importance of their component species. At this stage, however, little work has addressed this aspect of arboreal ant biology (but see Majer, 1990; Stork, 1991).

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In this paper I characterize for the first time the entire ant fauna of a small patch of tropical rainforest canopy in terms of both its taxonomic composition and of the numbers and biomass of the component species. This effort grew out of an attempt to determine the numbers of arthropod specimens and species per major taxon in a small, discrete patch of tropical forest canopy surrounding the Pakitza research station in Manu National Park, Madre de Dios, Peru (Erwin, 1989a, 1989b). Erwin reported already on these collections, and summarized data on the relative abundance of the major arthropod groups based on about two-thirds of the total sample (Erwin, 1989b). After nearly 82,400 arthropods had been sorted, 69.6% of these were ants. The rest of the arthropods were primarily beetles (9.1%), psocopterans (4.0%), dipterans (2.5%), collembolans (2.2%), and spiders (2.0%). A preliminary report on the ants in these collections, based on partial samples, was published already (Tobin, 1991). This paper represents a final report based on the entire ant fauna, and contains a complete species list including changes resulting from recent taxonomic revisions (e.g., Shattuck, 1992).

Little has been published on the relative importance of the component species in arboreal ant assemblages, and there are few studies of the taxonomic composition of point samples that can be used for comparison with this study. Wilson (1987) found 43 ant species in 26 genera in a single tree in Tambopata, Peru. Harada and Adis (1994), working in Brazilian Amazonia, sampled a number of trees and found as many as 77 species in individual trees. Tobin (ms.) found between 22 and 44 species in point samples collected along a transect in central Panama. These figures appear to be larger than comparable ones for Asia (Stork, 1991) and Australia (Majer, 1990).

On first impression, the extreme skew in the ranked species abundance in this sample appears to be extraordinary. One species comprises the majority of the numbers and biomass in the sample. The steep distribution includes a very long tail of species represented by numbers and/or biomass that are trivially small. This stands in contrast to the shallower, more equitable distribution of other tropical canopy arthropods such as beetles (Morse et al., 1988). I will argue, however, that the unusual distribution of ant species abundances may be an artifact of the spatial scale of the sample.

#### METHODS

A discrete patch of canopy, consisting of two adjacent trees and eleven associated vines, was selected for sampling. The trees were identified as *Matisia cordata* (Bombacaceae) and *Hirtella triandra* (Chrysobalanaceae). In selecting the sampling area, the aim was to maximize the diversity of arthropods in the resulting point sample; thus the size and structural complexity of the trees, and the amount of associated epiphytic growth, were the main criteria used. A total of 93.6 m<sup>2</sup> (1008 square feet) of plastic sheeting was hung in the understory to collect the falling specimens, and the selected area of canopy was treated with insecticidal fog (Erwin, 1983a, 1983b, 1989a). The resulting specimens were preserved in 70% ethanol for subsequent sorting and processing.

In the lab, the arthropods in the sample were sorted to order, with the exception of the family Formicidae, which was separated from the rest of the Hymenoptera

(Erwin, 1989a, 1989b). Following this first sort, I sorted the ants to species. Species determinations were made at the Museum of Comparative Zoology (M.C.Z.), Harvard University, on the basis of comparisons with available specimens and of published and unpublished keys. Voucher specimens are deposited at the M.C.Z.

Following the identifications, biomass and the numbers of individuals were determined for each species. For species with less than approximately 500 workers, the number of individuals was determined by direct counts or estimated from subsamples. Biomass was estimated based on the number of workers and the average dry weight of specimens of each species or of other species of similar size and body type. For the most abundant species, biomass was determined directly by weighing all the specimens of each species; the number of specimens per species was estimated from the total biomass of each species and the average dry weight of workers of that species. Samples were dried at 60°C until weight was stable.

#### RESULTS

A total of 85 ant species belonging to 29 genera and 5 subfamilies were found in the samples (Table 1). One species, *Dolichoderus bispinosus* (formerly known as *Monacis bispinosa*; Shattuck, 1992), dominated the sample, comprising approximately 65% of the biomass and 69% of the individuals in the collection (Table 2). Only four species (*Dolichoderus bispinosus*, *Dolichoderus decollatus*, *Azteca* sp. 1, and *Paraponera clavata*) contributed more than 1.0 g to total biomass (dry weight). Other important species were *Anochetus* sp. nov., *Pachycondyla* sp. 1, and *Camponotus* sp. 3. The contribution to biomass of the majority of species in the sample was trivial, amounting to no more than a few milligrams (Fig. 1). In addition, 1.43 g of assorted ant brood were found in the sample; these have not been included in Table 2.

In terms of numbers, the dominant species were *D. bispinosus* (43,200 workers), *Azteca* sp. 1 (14,500), *D. decollatus* (1,620), and *Azteca* sp. 2 (1,560). All other species were represented by fewer than 1,000 individuals. Among these nondominant species are, in decreasing order of abundance, *Crematogaster* sp. 1, *Solenopsis* sp. 4, *Tapinoma* sp. 1, *Solenopsis* sp. 3, and *Anochetus* sp. nov. Of these, only *Anochetus* sp. nov. made a contribution of more than 1% to total biomass. Fifty-one species, or nearly 60% of the total, were represented by ten or fewer individuals.

#### DISCUSSION

A large body of evidence documents the critical role of competition in determining ant community structure in a wide variety of habitats (Hölldobler and Wilson, 1990 and references therein). Numerous studies have documented dominance hierarchies in which certain species predictably displace others from foraging and nesting sites (e.g., Vepsäläinen and Pisarski, 1982; Savolainen and Vepsäläinen, 1988). Research on the spatial distribution of ant territories in tropical canopies has invoked competition to explain the commonly observed pattern of territorial exclusion by dominant species, known as an ant mosaic (Room, 1971; Majer, 1972; Leston, 1978; reviewed by Jackson, 1984). Under this view, colonies of dominant species partition the canopy into a series of mutually exclusive territories, and each of these codominant species is positively or negatively associated with a series of nondominant

Table 1. Ant species collected in trees nos. 12 and 13, Zone 02/18/08, Pakitza, Manu National Park, Madre de Dios, Peru. A total of 85 species in 29 genera were found.

<b>PONERINAE</b>	<b>DOLICHODERINAE</b>
<i>Anochetus</i> sp. nov.	<i>Azteca</i> sp. 1
<i>Gnamptogenys acuta</i>	<i>A.</i> sp. 2
<i>G. concinna</i>	<i>Dolichoderus attelaboides</i>
<i>Hypoponera</i> sp. 1	<i>D. bidens</i>
<i>H.</i> sp. 2	<i>D. bispinosus</i>
<i>Odontomachus haematodus</i>	<i>D. decollatus</i>
<i>Pachycondyla cavinodis</i>	<i>D. diversus</i>
<i>P. crenata</i>	<i>D. lutosus</i>
<i>P. unidentata</i>	
<i>P.</i> sp. 1	<b>MYRMICINAE</b>
<i>Paraponera clavata</i>	<i>Allomerus octoarticulatus</i>
	<i>Crematogaster</i> sp. 1
<b>FORMICINAE</b>	<i>C.</i> sp. 2
<i>Brachymyrmex</i> sp. 1	<i>C.</i> sp. 3
<i>B.</i> sp. 2	<i>C.</i> sp. 4
<i>Camponotus bideus</i>	<i>Cyphomyrmex</i> sp. 1
<i>C. bradleyi</i>	<i>Leptothorax anduzei</i>
<i>C. heathi</i>	<i>L.</i> sp. 1
<i>C. lancifer</i>	<i>Ochetomyrmex</i> sp. 1
<i>C. latangulus</i>	<i>Pheidole</i> sp. 1
<i>C. novogranadensis</i>	<i>P.</i> sp. 2
<i>C.</i> sp. 1	<i>P.</i> sp. 3
<i>C.</i> sp. 2	<i>P.</i> sp. 4
<i>C.</i> sp. 3	<i>P.</i> sp. 5
<i>C.</i> sp. 4	<i>P.</i> sp. 6
<i>C.</i> sp. 5	<i>P.</i> sp. 7
<i>C.</i> sp. 6	<i>P.</i> sp. 8
<i>C.</i> sp. 7	<i>P.</i> sp. 9
<i>C.</i> sp. 8	<i>P.</i> sp. 10
<i>C.</i> sp. 9	<i>P.</i> sp. 11
<i>C.</i> sp. 10	<i>Procryptocerus</i> sp. 1
<i>Dendromyrmex fabricii</i>	<i>Rogeria</i> sp. 1
<i>Myrmelachista</i> sp. 1	<i>Sericomyrmex</i> sp. 1
<i>Paratrechina</i> sp. 1	<i>Smithistruma</i> sp. 1
	<i>Solenopsis</i> sp. 1
<b>PSEUDOMYRMECINAE</b>	<i>S.</i> sp. 2
<i>Pseudomyrmex browni</i>	<i>S.</i> sp. 3
<i>P. dendroicus</i>	<i>S.</i> sp. 4
<i>P. godmani</i>	<i>S.</i> sp. 5
<i>P. laevifrons</i>	<i>Strumigenys subdentata</i>
<i>P. oculatus</i>	<i>Wasmannia auropunctata</i>
<i>P. pupa</i>	<i>Zacryptocerus</i> sp. 1
<i>P. simplex</i>	<i>Z.</i> sp. 2
<i>P. tenuis</i>	<i>Tapinoma</i> sp. 1
<i>P. tenuissimus</i>	<i>T.</i> sp. 2
<i>P.</i> sp. 1	

Table 2. Biomass and numbers of dominant ant species.

Species	Biomass (grams)	% Total biomass	Number of individuals <sup>1</sup>	% Total numbers
<i>Dolichoderus bispinosus</i>	31.51	64.2	43,200	69.0
<i>Dolichoderus decollatus</i>	11.68	23.8	1,620	2.6
<i>Azteca</i> sp. 1	1.67	3.4	14,500	23.1
<i>Paraponera clavata</i>	1.39	2.9	20	n.c. <sup>2</sup>
All other species <sup>3</sup>	2.80	5.7	3,300	5.3
Total	49.05	100.0	62,640	100.0

<sup>1</sup> The numbers in this column are estimates based on subsamples.

<sup>2</sup> *P. clavata* made a negligible contribution to numbers.

<sup>3</sup> This includes 81 species represented in the collections by workers and/or queens.

species. Thus dominant ants are seen as the major determinants of ant community structure.

Most ant mosaic research, however, has been carried out in tropical agroecosystems (principally in cacao plantations), which lack the structural and ecological complexity of natural forest canopies. To what extent principles derived from ant mosaic theory might be generalizable to natural forest canopies has been a matter of some controversy. Leston (1978) working in a forest near Bahia, Brazil, showed that dominant canopy ant species hold mutually exclusive territories and form a three-dimensional mosaic. In natural forest canopies, then, dominants are present and competition may determine the spatial distribution of dominant ant species *inter se*, as it does in

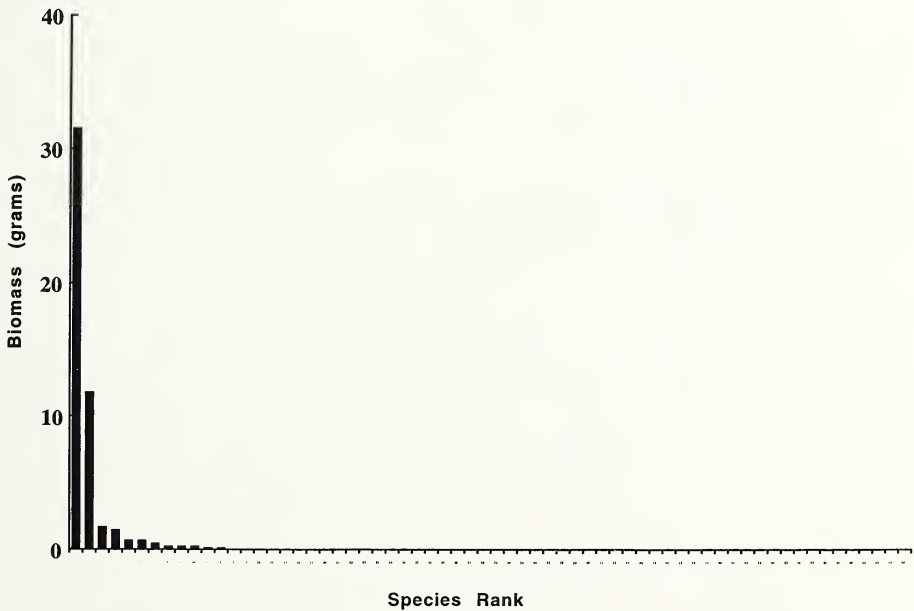


Fig. 1. Ranked species: Abundance plot.



tropical plantations. However, the little available evidence from natural forests does not tell us to what extent dominants may be the organizing agents vis-à-vis the nondominant species, which comprise the majority of the species richness. The evidence I present here, as well as evidence from natural forest canopies in Panama (Tobin, ms.), strongly indicates that dominant ant species do not determine ant community composition as a whole in undisturbed tropical rainforest canopies.

That dominant species do not always determine the composition and structure of canopy ant assemblages is suggested by a striking feature of the data presented in this and earlier, comparable studies. A surprisingly high fraction of the total ant species richness at a site can be found in any point sample collected at that site. For example, Wilson (1987) reported finding 135 species in an extensive series of collections across four forest types in the Tambopata Reserved Zone, Peru. In one, particularly diverse point sample he found 46 species, or nearly 35% of the entire fauna; only 6 of those species were not found in other samples from the area. Tobin (ms.), working in Panama, found that as many as 39% of the ant species in an extensive series of collections were found in a single point sample. Also, numerous species were present in a large number of samples irrespective of the dominant species in the sample. Thus dominant ant species are not linked to a few co-occurring nondominant species, as in classical ant mosaics. The picture that emerges is one of a mosaic of mutually exclusive dominant species superimposed upon an assemblage of species that are found throughout the forest but only in small numbers and biomass. This assemblage of nondominants appears, at least to some extent, to exist irrespective of the presence or absence of the dominant species.

The diverse assemblage of nondominant species raises important questions. Wilson (1987), upon documenting the coexistence of 43 species of ants in one point sample, asked how it was possible for so many species to occupy the same site. With nearly twice that number of species in the present study, the question seems all the more pressing. One possibility is that many nondominants are not territorial, and are coexisting by means that do not involve aggressive mutual exclusion, thus allowing higher local diversities. This is almost certainly true in part. The spatial scale of canopy foggings, however, may be too coarse to resolve ant mosaics of small nondominant species, to the extent that they exist. Competition may still play a role in structuring assemblages of nondominant ants that is presently invisible, given our current sampling methods.

The data in the present study reveal a local ant assemblage in which one species preempts over two-thirds of the biomass space, the amount of biomass that an assemblage can sustain given the energy entering the system and the conversion efficiencies of its component species (Tobin, 1994) (Fig. 1). While puzzling, this degree of dominance is a natural consequence of the spatial scales of both the dominant ant mosaics and the sampling regime in the present study. As seen already, a typical canopy sample, covering an area of approximately 100 m<sup>2</sup>, may reveal 25-50% of the total ant fauna of the area but only one or a small number of dominants. A second fogging sample would expose a few more nondominants in the tail of the species abundance distribution, but may reveal an entirely different dominant species.

As similar samples are pooled, the tail of the distribution might only be between two and four times as long as that of the original sample, but a number of other dominant species would be revealed. The effect of this pooling would be to fill out the left side of the distribution without greatly increasing the length of the tail, thus

reducing its skewness and making it comparable to other, more typical distributions. Hence the scale of individual fogging samples, though large in terms of the number of individual arthropods collected, is too small to reveal the true species abundance distribution of an area.

The ultimate explanation for high local ant diversity may reside in the extreme structural complexity of the canopy environment itself (Lawton, 1983, 1986; Morse *et al.*, 1985; Gunnarsson, 1992; see also Terborgh, 1985). Abiotic factors, such as temperature and humidity, range widely from the forest floor to the canopy (Parker, 1995), and different levels of the canopy are associated with different epiphytes and their attendant arthropod faunas. Epiphytic cacti may be common in the same forest that is thick with ferns near the ground. From the point of view of sensitive plants and small arthropods, then, the range of conditions along this altitudinal gradient results not in a single, homogeneous canopy habitat but in a series of more or less distinguishable microhabitats superimposed upon each other from the understory to the high canopy. As in the case of the marine intertidal, alpha diversity in a tropical forest canopy may be more a function of a gradient of physical conditions over a small distance which can be finely partitioned, than of any one set of conditions in particular.

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